CONGRUENCE BETWEEN ALLOMETRIC COEFFICIENTS AND PHYLOGENY IN STIPOID GRASSES: AN EVO-DEVO STUDY

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ABSTRACT

There is a strong, highly significant relationship between relative growth rates, in Stipoid grasses, as represented by allometric coefficients, derived from one set of spikelet variables, and a phylogenetic classification derived from an independent set of variables. Differences among allometric coefficients can be related to the specific histogenetic events underlying grass development. A relationship between ontogeny and phylogeny argues for a causal connection between the two, a connection that is thermodynamic in nature. In ontogeny there is the generation of information, i.e., matter transformation, which accompanies energy dynamics in organisms as they develop. In species information is generated through the appearance of unique developmental events in individuals in the species as well as genetically, i.e., mutation, recombination and chromosomal changes. In both instances the generation of this information is historically constrained. The information system of a species is virtual, known only through its effect on the organisms that appear. Also, this virtual information means the information produced when an individual develops is just a small subset of the potential information. As the information system of a species expands through unique developmental and genetic events, it becomes unstable leading to speciation.

RESUMEN

Hay una relación fuerte, altamente significativa entre las tasas de crecimiento relativo, en gramíneas estipoides, como las representadas por coeficientes alométricos, derivados de un conjunto de variables de la espiguilla, y una clasificación filogenética derivada de un conjunto independiente de variables. Las diferencias entre coeficientes alométricos pueden relacionarse con eventos específicos histogenéticos del desarrollo de las gramíneas. Una relación entre ontogenia y filogenia aboga por una conexión causal entre las dos, una conexión que es de naturaleza termodinámica. En la ontogenia existe la generación de información, ej., transformación de la materia, que acompaña a la dinámica de la energía en los organismos mientras se desarrollan. En las especies la información se genera mediante la aparición de eventos de desarrollo únicos en individuos de las especies así como asgenéticamente, ej., mutación, recombinación y cambios cromosomáticos. En ambas instancias la generación de esta información está constreñida históricamente. El sistema de información de una especie es virtual, conocida sólo por sus efectos en los organismos en los que aparece. También, esta información virtual significa que la información producida cuando un individuo se desarrolla es sólo un pequeño subconjunto de la información potencial. A medida que el sistema de información de una especie se expande mediante eventos genéticos y de desarrollo únicos, se hace inestable dando lugar a la especiación.

INTRODUCTION

The idea of a relationship between evolution and development is as old as evolution itself (Gilbert 2003) even used by Darwin (1859) as evidence for unity of type (Gilbert 2003). In the middle of the 20th century the rise of the Modern Synthesis resulted in genetics supplanting development as an explanatory phenomenon and it was argued that genetics and not development held the key to evolution (Gilbert 2003). In spite of genetic ideas coming to dominate in evolutionary studies, a relationship between development and evolution was not abandoned. For example, evolution, as descent with modification, formed the conceptual basis in attempts to understand the basic structure of the flower (e.g., Barnard 1957, 1960; Tepfer 1953; Tucker 1959) or of vascular plants in general (Meeuse 1966). Gould's *Ontogeny and Phylogeny* (1977) emphasized the relationship between the two phenomena and stimulated studies wherein evolutionary change was described in terms of modified allometries (see e.g., Gibson & Diggle 1997). There were also attempts to link evolution and development through emphasizing the developmental changes that have occurred with evolution (see McMahon & Hufford 2002; Olson 2003; Richards et al. 2006 and references therein). Still another approach to linking development and evolution described the changes in relative frequency of histogenetic events, e.g., cell division and enlargement, that occur with evolution (Kam & Maze 1974; Maze et al. 1972; Stebbins 1967).

Three developments in biology led to a renewed interest in the relationship between evolution and development (Gilbert 2003). One was the ability to infer more precise phylogenetic relationships based on numerical analyses of molecular data (Soltis et al. 2000). The second was the identification of genes involved in the development of organisms. Once these genes were known mutations in them could be used to determine their role in developmental processes, such as the nature (see Friedman et al. 2004; Meyerowitz 2002) or positioning (Smith et al. 2006) of appendages. In addition information was obtained on how genetically mediated changes affected growth rates which, in turn, are expressed phenotypically as changes in size and shape (Coen et al. 2004; Langlade et al. 2005; Rolland-Lagan et al. 2005). The third development resulted from re-evaluation of basic precepts and led to a conclusion of "..the inability of the neoDarwinian synthesis to account for many phenomena of higher-level phenotypic organization" (Müller & Newman 2005a). Similar arguments were presented in Maze & Finnegan (2008).

Modern studies in evolutionary development (evo-devo) include those which address the incorporation of developmental traits, either structural (see Olson 2003; Friedman et al. 2004) or molecular (Arendt 2003) in established phylogenetic trees or the genetic changes underlying adaptation (Hoekstra & Coyne 2007). Evo-devo arguments have also been used to explain the origin of novelty as being the result of environmentally induced developmental events (Müller & Newman 2005b; West-Eberhand 2005) that become incorporated into the DNA. Jablonka & Lamb (1995) and Steele et al. (1998) have also argued for the incorporation of environmentally induced traits. Pigliucci (2007), as well, has raised the question of the necessity of an extended evolutionary synthesis which incorporates environmental changes more directly into accounts of evolutionary change.

Another series of studies linking evolution and development are those seeking a common underlying cause in this case in non-equilibrium thermodynamics and information theory (Maze 1999; Maze et al.. 1990, 2001a,b, 2002, 2003a,b, 2005; Robson et al. 1993). In these studies it was reasoned that the morphological changes that occur with both evolution and development are the result the transformation of matter, i.e., the production of information, through which energy dynamics are carried out. This is seen, for example, in the production of high energy compounds such as ATP and NADH or carbohydrates, cellulose, secondary metabolites and proteins. The basic argument is that as matter is transformed during development it can be understood as information, "in-formed matter". This new morphological organization of information becomes part of the totality of information that delineates a species, i.e., its information system (Brooks, 2001, 2002; Brooks & Wiley 1988; Maze et al. 2005). This results in the expansion of the information system due to matter transformation and that, along with the addition of new information through genetic mutation and recombination, results in an increase in the complexity of the information system of a species. Once the information system of a species reaches a certain stage of complexity it bifurcates, expressed biologically as speciation (Brooks, 2001; Brooks & Wiley 1988). This view of speciation, admittedly a unique one, has been tested and verified (Maze et al. 2005).

Here I take a different approach to the study of evolution and development, a comparison of the relationships inferred from a phylogeny with the relationships inferred from an analysis of growth phenomena represented by allometric coefficients. There is no doubt that there is some sort of relationship between allometric coefficients and evolutionary change (Coen et al. 2004; Langlade et al. 2005; Rolland-Lagan et al. 2005); see also Gould (1977). But, what is the nature of that relationship beyond the truism that taxa differ in their allometric coefficients? Specifically I explore the idea there is some sort of predictability between allometric coefficients and phylogeny. In other words, by knowing one, e. g., allometric coefficients, can some sort of predictive statement be made about phylogeny? A predictive relationship between allometric coefficients and phylogeny is of interest as it may indicate some deep-seated underlying cause such as was argued by Maze (1999); Maze et al. (1990, 2001a,b, 2002, 2003a,b, 2005) and Robson et al. (1993).

MATERIALS AND METHODS

Plants. The plants used in this study are grasses in the genus *Achnatherum*, tribe Stipeae (Poaceae: Pooideae).

They are: *A. lemmonii* (Vasey) Barkworth, *A. nelsonii* (Scribner) Barkworth, *A. occidentale* (Thurb. ex S. Wats.) Barkworth, *A. hendersonii* (Vasey) Barkworth and *A. wallowaense* Maze and Robson; the specific collections are in Table 1. All are indigenous to western North America (Hitchcock, et al., 1969). The first three are wide-spread; the last two are more restricted in distribution; *A. hendersonii* occurs in central Washington and central Oregon, *A. wallowaense* in central and northeastern Oregon. These two species grow only in scattered sites where a very shallow, ca. 15 cm to bedrock, soil is subject to frost-heaving and at least one, *A. hendersonii* appears to be adapted to such a habitat as a result of the combination of a slower growth rate (Binney & Bradfield 2000) and unique root structure (Maze 1981). Similar studies have not been done on *A. wallowaense* but its close relationship between *A. hendersonii* and its occurrence in a similar habitat make me believe its growth and root structure would be the same as *A. hendersonii*.

The plants studied were collected from natural populations and not from a common garden. The latter would be desirable as a means of minimizing environmentally induced morphological variation but I lack the resources to establish such. Also, even though plants may be grown in a common garden the environmental factors that may cause differences among plants can not be completely eliminated; a common garden cannot eliminate all micro-environmental variation due to heterogeneity in the size of soil particles or the distribution of chemicals, water or other organisms, particularly microorganisms. This problem might be alleviated with random plots but the sample sizes required for this study preclude that. Second, interpreting the response of *A. hendersonii* or *A. wallowaense* in a common garden would be difficult because their native habitat is so odd. The ideal, of course, would be reciprocal transplant experiments but it is unlikely that *A. occidentale*, *A. nelsonii* and *A. lemmonii* could survive the solifluction seen in the habitats where *A. wallowaenes* and *A. hendersonii* occur.

The basic units of collection were individual plants and 47 spikelets were measured from each. The individuals were, in turn, organized into populations of 8–12 individuals and the populations into species of 2–6 populations per species. The number of individuals per populations and populations per species was the result of the sampling method required to do this study. To make a statistical comparison between allometric coefficients and a phylogeny I generated several sets of allometric coefficients for each species. This, in turn, requires enough spikelets to assure the calculated allometric coefficients were stable and not artifacts of small sample size. For details see analyses. 7473 spikelets were measured for this study.

The grasses studied here offer certain advantages. First, having one floret per spikelet, the structure and its parts are easy to identify and measure thereby assuring that homologous variables were being measured. Second, there is a body of developmental data on the Stipeae (Kam 1974; Kam & Maze 1974; Maze et al. 1971, 1972; Mehlenbacher 1970) which allows for connections to be made between allometric coefficients and histogenetic events that occur during ontogeny.

Variables. Five variables were measured for each spikelet: length of the two glumes, floret length and width and awn length, variables adequate to describe the spikelets. The relatively restricted set of variables was the result of a tradeoff between spikelet description and the number of spikelets necessary to make the required calculations . The results from these five variables are the same as those from a more expanded set of variables in another study on the Stipeae that also included the width of the glumes (Maze et al. 2003b).

Allometric coefficients. The first step in generating allometric coefficients was, for each species, to do a series of PCAs on a variance/covariance matrix of $\log_{10}$ transformed variables. The first eigenvectors of such an analysis is a vector of allometric coefficients (Jolicoeur & Mosimann 1960) that describe the relationship between each variable measured and the first PCA axis. These allometric coefficients represent a measure of the relationship between development of the variable measured and time, as represented by the first PCA axis (Jolicoeur & Mosimann 1960). There are a couple of problems with this approach. First, it is mature structures that are measured and not their development. Second, a first PCA axis, often a size axis, is not a perfect substitute for time. However, in a study like this these problems must be acknowledged, lived with and adjusted for. The demands of sample size preclude directly assessing developmental time which requires sections of spikelets at various stages of development. There are four problems with doing

TABLE 1. Species and collections used. Numbers by acronym for each collection, number of individuals measured.

Achnatherum lemmonii

LEMENT1–8. 28.3 km n Enterprise on Oregon State Highway 3, Wallowa Co., OR, U. S. A.; plants growing in forest of ponderosa pine and Douglas fir. 45.80 N, 117.21W. 9 Jul 1998

LEMCOLO1–8. just across Kittitas-Chelan Co. line in Kittitas Co. along Colockum Pass Road, WA, U. S. A.; plants growing in an open stand of ponderosa pine. 47.50N, 120.19W. 13 Jun 2002.

LEMFOX1–8. 7 km from U. S. Forest Service Road 4240 on road 200, Crook Co., OR, U. S. A.; plants in deep soil in among ponderosa pine. 44.16N, 120.10W. 15 Jun 2002.

LEMIND1–8. 15.8 km s. Foothill Road on Indian Springs Road, Twin Falls., Co., ID, U. S. A.; plants growing among shrubs in rolling hills. 42.34N, 114.57W. 11 Jun 2004.

LEMSIE1–8. 2.4 km. s. of Graeagle on Calif. St. Highway 89, Plumas Co., CA, U. S. A.; plants growing with ponderosa pine. 39.45N, 120.37W. 18 Jun 2004.

LEMCLR1–6. 1 km. W. of Calif. St. Highway 89, On Clark Creek Road, Shasta Co., CA, U. S. A.; plants growing with Quercus kellogii and ponderosa pine. 41.15N, 121.72W. 19 Jun 2004.

Achnatherum hendersonii

HENCOL1–8. along Tarpescan Creek Road where it joins Colockum Pass Road, Kittitas Co., WA, U. S. A.; plants growing in shallow soil in sparse vegetation. 47.47N, 120.20W. 13 Jun 2002.

HENFOX1–8. 7 km from U. S. Forest Service Road 4240 on road 200, Crook Co., OR, U. S. A.; plants growing in shallow soil in sparse vegetation. 44.30N, 120.20W. 15 Jun 2002

Achnatherum wallowaense

WALBON1–8. near Boner Springs, middle sw ¼ of se ¼ of section 24, T3N, R45E., Wallowa-Whitman Nat. For., along FS Road 46, Wallowa Co, OR, U. S. A.; plants growing in shallow soil in sparse vegetation. 45.67N X 117.13W. 26 Jun 1993.

WALSKO1–8. middle of section 9, T12S, R18E, Ochoco N. F., Crook Co., OR, U. S. A.; plants growing in shallow soil in sparse vegetation. Site 30011 USDA Forest Service R-6 Threatened, Endangered and Sensitive Plant Surveys. 44.53N X 120.60W, 28, 29 Jun 2003.

Achnatherum occidentale

ELMSIE1–10. 2.4 km. s. of Graeagle on Calif. St. Highway 89, Plumas Co., CA, U. S. A.; plants growing with ponderosa pine. 39.45N, 120.37W. 1 Jun 2001.

ELMBUL1–8. growing along old road just n. of Bull Mountain near cattle guard on Forest Service Road 2730, 2 miles from Forest Service Road 27, Ochoco National Forest, Crook Co. OR, U. S. A. 44.51N, 120.60W. 15 Jun 2002.

ELMCOL1–8. along west bank Columbia River just north of bridge carrying U. S. Highway 395 across the Columbia River, Stevens Co., WA, U. S. A.; plants growing with ponderosa pine. 48.63N, 118.13W. 18 Jun 2002.

ELMMON1–8. n. side Power House Road, just across U. S. Highway 395 on the west bound extension of Calif. St. Hiway 167, Mono Co., CA, U. S. A.; plants growing in sage brush. 38.05N, 119.17W. 17 Jun 2004.

ELMOLD1–8. 1.6 km sw junction California State Highways 44 and 89 on 89, near Old Station, Shasta Co., CA, U. S. A. 40.68N, 121.30W. 19 Jun 2004.

Achnatherum nelsonii

NELWL1–14. from 1.1 km w. of Highway 97 on White Lake Road, s. of Pentiction B. C., Canada; plants growing open area with ponderosa pine. 49.42N, 119.64W. 8 Jun 2001.

NELCOL1–8. from along west bank Columbia River just north of bridge carrying U. S. Highway 395 across the Columbia River, Stevens Co., WA, U. S. A.; plants growing with ponderosa pine. 48.63N, 118.13W. 18 Jun 2002.

NELENT1–3. from 28.3 km n Enterprise on Oregon State Highway 3, Wallowa Co., OR, U. S. A.; plants growing in forest of ponderosa pine and Douglas fir. 45.80 N, 117.21W. 9 Jul 1998

NELANA1–8 *A. nelsonii* from rest stop on Anacharist Mt. Along Highway 3, British Columbia, Canada. 49.02N, 119.37W. Jun 2002.

NELMAN1–8 growing in gravel patch in parking lot at start of Beaver Pond Nature Trail, Manning Prov.Park, British Columbia, B. C., Canada. 49.06N, 120.75W. 3 Jul 2004

that. First, it would mean that the number of spikelets from an individual that could be measured is limited since the direct assessment of time demands destructive sampling. Second, this would be extremelhy time consuming since the preparation of spikelets of different ages requires the production of a large number of microscope sections. Third, the lack of synchrony between developmental stages in the Stipeae (Maze et al. 1971, 1972) would introduce a problem in comparing spikelets of different ages. Fourth, the inability of get sections that could be easily measured means that far less data could be gathered.

In order to make comparisons between development, as represented by allometric coefficients, and phylogeny, as represented by a phylogenetic classification I had to represent each species using allometric coefficients as variables. That is easily done, do the required PCA for each species, take the first eigenvector and then transpose it from a vector into a row of five variables where each variable, say first glume length, is represented by its allometric coefficient. But it would be inappropriate to do a single PCA for each species. Such would result in a data set with only five cases, one for each species, and five variables, the allometric coefficients for the five features measured. Such a small data set is of little use in a comparison with the results of a phylogenetic analysis since it is too small of a data set to produce meaningful results. Thus, to generate a population of allometric coefficients for each species, I randomized all the spikelets within each species, divided that randomized data set into groups of 94 spikelets each and did a PCA on each of those groups. This meant that there were from 8 PCAs, for *A. hendersonii* and *A. wallowaense*, 20 for *A. occidentale*, 21 for *A. nelsonii* and 23 sets for *A. lemmonii*. Each group of 94 was checked to assure that all individuals and populations collected for each species were included within it. A group size of 94 was chosen to assure analytical stability, i.e., that the results were not an artifact of small sample size.

The randomization of spikelets was a choice made on developmental considerations. Allometric coefficients for any set of spikelets are a numrical summary of the developmental events of the spikelets in that set. Those developmental events will be the result of the genomic instructions for development and the interactions between that genome and the environment it experiences during development. That environment has both external and internal components. The external environmental factors producing an effect would be the likes of the continually changing day length, temperature, moisture, soil and neighboring organisms that a developing plant experiences. The internal environment is established by the distribution of growth promoting and inhibiting substances, e.g., hormones. The complexity of the internal environment can be traced to the continually changing sources of growth effecting substances as growth centers appear and disappear. The purpose of data randomization was to neutralize the effect of the genotype of any one individual as well as any environmental effect on calculated allometric coefficients. Each 94 spikelet sample included spikelets from all individuals and populations. Thus, any one of the sets would not have spikelets that have all been subjected to similar environmental, both internal and external, or genetic effects. This lowers the probability that any one PCA was biased because of an asymmetric distribution of environmental influences.

As a result of the randomization within each species, subdividing of the data for each species into groups of 94 spikelets and submitting each group to PCA, I generated an 80 x 5 matrix. Each of the 80 cases represents the results of one PCA of the randomized 94 spikelets and the five variables were the allometric coefficients i.e., the elements in first eigenvector for that PCA. The allometric coefficients were compared with each other using the Kolomogorov-Smirnov test of variables. This is a test to determine if two variables have a similar distribution as based on a distance function. This distance statistic was used to evaluate the relationship among the allometric coefficients, a small distance indicating a similar distribution is taken as evidence the allometric coefficients for the variables are similar. The similarity and differences among the allometric coefficients were then evaluated by relying on the ontogenetic events whereby the different variables develop. Variables with similar allometric coefficients would be expected to show similar ontogenetic events, e.g., patterns of cell division and maturation in comparable tissues.

Phylogenetic analyses. The phylogenetic analyses were based on 19 variables of both vegetative and reproductive features (Table 2). To avoid analytical redundancy variables that described the features similar to those used to calculate allometric coefficients were not included in the phylogenetic analysis. Although there were only five species subjected to phylogenetic analysis, I wanted to be sure the phylogenetic signal was strong, i.e., that the data describing the five species was sufficiently stable to give the same results regardless of outgroup. To that end, four species were used as outgroups, *Hesperostipa comata* (Trin. & Rupr.) Barkworth, *Nasella viridula* (Trin.) Barkworth, *Achnatherum lettermanii* (Vasey) Barkworth and *A. hymenoides* (Roem. & J.A. Schult.) Barkworth. The first two species are, like *Achnatherum*, in the Stipeae and, at one

TABLE 2. Characters used for phylogenetic analysis and their codes.

1 Height: >4 dm – 0, <4 dm – 1
2 Sheath: not villous at throat – 0, villous at throat – 1
3 Ligule: acuminate – 0, acute – 1, collar shaped – 2
4 Blade length: >8 cm – 0 <8 cm – 1
5 Blade width: >3.5 mm – 0, 3.4 to 1 mm – 1
6 Inflorescence shape: open – 0, closed - 1
7 Inflorescence length: >8 cm – 0, < 8 cm – 1
8 Inflorescence branches: stiff – 0, lax – 1
9 Glume shape: narrow – 0, wide – 1
10 Glume tip: strongly acuminate – 0, acuminate – 1, acute – 2
11 Lemma: thin – 0, indurate – 1
12 Lemma apex: straight – 0, angled – 1
13 Callus shape: curved – 0, straight - 1
14 Callus length: >3 mm – 0, 3 to 1 mm – 1, <1mm – 2
15 Callus tip: sharp – 0, blunt – 1
16 Awn pubescence: scabrous to hirtellous – 0, long pubescent – 1
17 Awn persistence: persistent – 0, tardily deciduous – 1, deciduous – 2
18 Palea:lemma: subequal – 0, shorter – 1
19 Palea pubescence: pubescent – 0, glabrous – 1

time were congeneric, as *Stipa*, with four of the five species, *A. lemmonii*, *A. occidentale*, *A. hendersonii* and *A. nelsonii*, studied here. The other two are more closely related to the five species studied here. Single species were used to polarize the data since doing so meant that a larger set of variables could be used in constructing a phylogeny than if a genus or other group of closely related species was used to polarize the data. Phylogenetic analyses were performed with Phylogenetic Analyses Using Parsimony (PAUP) Version 4.0 b10.6 (Sinauer Associates Inc. Sunderland, MA) using an exhaustive search with equal character state weighting. It would be desirable to use molecular data, but molecular data is available for only a limited set of the species used here (Jacobs et al. 2000).

All the separate phylogenetic analyses that were produced using the four different outgroups recognized the same three lineages, one consisting of *A. nelsonii* and *A. occidentale*, another of *A. hendersonii* and *A. wallowaense* and the third being the pair *A. hendersonii* and *A. wallowaense* along with *A. lemmonii*. These groupings are consistent with existing data. *Achnatherum nelsonii* and *A. occidentale* are putatively closely related and have been considered, in the past, to be varieties of one species (Hitchcock et al., 1969). *Achnatherum lemmonii* and *A. hendersonii* share some unique developmental features including obliquely directed tissue at the apex of the lemma resulting from periclinal divisions in the protoderm producing an oblique floret apex, an extension of the outer integument that projects into the stylar canal and a distinctive pattern of cell enlargement in the callus (Maze et al. 1972; Mehlenbacher 1970). *Achnatherum wallowaense* has not been studied developmentally but the strong morphological similarity between it and *A. hendersonii* (small indurate, glabrous floret with a blunt callus, oblique floret apex, long palea and weak, easily deciduous awn) makes me suspect it has similar developmental features. A close relationship between *A. lemmonii* and *A. hendersonii* was reported by Jacobs et al. (2000). The same would be indicated by the hybrids formed between those two species (Spellenberg & Mehlenbacher 1971).

In order to compare the results of a phylogenetic analysis with allometric coefficients for the five species included in that phylogenetic analysis I generated a data matrix to describe the evolutionary structure inferred by the phylogenetic analysis. This data matrix consisted of three dummy variables and 80 cases, the same number of cases as in the data matrix of allometric coefficients. One dummy variable described the lineage consisting of *A. wallowaense* and *A. hendersonii*, another that consisting of *A. occidentale* and *A. nelsonii*, and the third the lineage of *A. lemmonii*, *A. hendersonii* and *A. wallowaense*. This matrix was joined to the matrix of allometric coefficients and the values ascribed to those dummy variables was determined

by the species in the matrix of allometric coefficients. The dummy variable that recognized the lineage consisting of *A. hendersonii* and *A. wallowaense* was given a value 2 for those instances where those two species in were positioned in the data matrix of allometric coefficients. Where the remainder of the species were positioned in the data matrix of allometric coefficients that dummy variable was given a value of 1. The value for the dummy variable used to represent the lineage consisting of *A. occidentale* and *A. nelsonii* was established in the same way; that variable was coded as 2 where those species were positioned in the data matrix of allometric coefficients and as 1 for the position occupied by the remainder of the species, *A. lemmonii, A. hendersonii* and *A. wallowaense*. The third dummy variable that represented the lineage consisting of *A. lemmonii*, *A. hendersonii*, and *A. wallowaense* was coded in the same way; it was given a value of two where those three species were positioned in the data matrix of allometric coefficients and a value of 1 elsewhere. An example of this matrix of dummy variables along with the species names is in Table 3.

Comparison. The first step in comparing the allometric coefficients with the phylogenetic classification was to summarize the data with principal components analysis (PCA). One PCA was done on the 80 x 5 data matrix of allometric coefficients and the other on the 80 x 3 matrix of dummy variables used to describe the phylogenetic classification. The results of the two PCAs were compared with a Spearman rank correlation coefficient. Only first PCA axes were compared since they are the best descriptors of the data. This approach gives a single number, statistical in nature, summarizing the relationship between development and evolution. A Spearman rank correlation coefficient was chosen because all the numerical manipulations I used made me leery of using a parametric statistic.

All analyses were done using SYSTAT 4.0 (Wilkinson 1991).

RESULTS

Table 4 presents a comparison of the allometric coefficients for the five species as a Kolomogorov-Smirnov test of variables. This statistic is a distance measure evaluating the distributions of the variables being tested. The distributions for the allometric coefficients for glume length have a distance that is not statistically significant. The distributions for all other pairs of variables have distances that are statistically significant. I interpret a statistically significant distance as an indication that the two variables are the result of events linked to their developmental history. I also did a Spearman rank correlation on the allometric coefficients. That is not shown but gave comparable results, the allometric coefficients for the lengths of the two glumes were the most strongly correlated.

The Spearman rank correlation coefficient between the PCA axis scores summarizing the allometric coefficients and the PCA axis scores summarizing the phylogenetic classification is .790, p<<<<.001; the allometric coefficients and phylogenetic classification are strongly congruent, they are giving similar signals. As a test of this approach I produced four other matrices of dummy variables describing classifications different from that inferred by the phylogenetic classification. The Spearman rank correlation between those four alternate classifications and the allometric coefficients were 0.030, -0.137, 0.579 and 0.413, all lower than the original test.

DISCUSSION

The similarity between the allometric coefficients for the length of the two glumes is hardly surprising. Although not all the species included here have been studied developmentally, those that have, *A. hendersonii* (Mehlenbacher 1970) and *A. lemmonii* (Maze et al. 1972), show very similar patterns in initiation and growth of the glumes. As well, the glumes of other Stipeae in which development has been described (Maze et al. 1971; Kam 1974; Kam & Maze 1974) are like *A. hendersonii* and *A. lemmonii*. The glumes are little more than acute to acuminate flaps of tissue without striking cellular differentiation in them other than relatively simple epidermis, parenchyma and vascular tissues.

The dissimilarity in allometric coefficients for all the other spikelet structures measured is, likewise, not surprising. Floret length, as measured here, is developmentally complex. One aspect of floret length,

TABLE 3. Abbreviated matrix of dummy variables that describe the evolutionary structure based on the phylogenetic classification. Species, the species in the data matrix of allometric coefficients, (number) is the number of cases for each species; LWH, dummy variable for lineage consisting of *A. lemmonii*, *A. wallowense* and *A. hendersonii*; NO, dummy variable for lineage consisting of *A. occidentale* and *A. nelsonii*; HW, dummy variable for lineage consisting of *A. hendersonii* and *A. wallowense*.

Species	LWH	NO	HW
Achnatherum lemmonii (23)	2	1	1
Achnatherum hendersonii (8)	2	1	2
Achnatherum wallowaense (8)	2	1	2
Achnatherum occidentale (20)	1	2	1
Achnatherum nelsonii (21)	1	2	1

TABLE 4. Kolmogorov-Smirnov two sample test results. Maximum differences for pairs of variables. G1L, length first glume; G2L, length second glume; FL, floret length; FW, floret width; AWN, awn length. ns, differences not significant; *, differences significant $p<.05 >.01$; ** $p<.01 >.001$; *** $p<.001$.

	G1L	G2L	FL	FW
G2L	0.188^{ns}			
FL	0.500^{***}	0.338^{***}		
FW	0.262^{**}	0.275^{**}	0.463^{***}	
AWN	0.325^{***}	0.350^{***}	0.637^{***}	0.250^{*}

the length of the lemma, is part of the integrated growth which leads to both the awn and the lemma. The first thing to initiate will become the awn, the tissue that will become the lemma appears after the awn when the awn-lemma primordium begins to spread around the floret apical meristem to form the lemma (Kam & Maze 1974 and references therein). Another developmental feature captured in floret length is the callus. This is marked by a unique, and often extensive, pattern of cell enlargement slightly oblique to the longitudinal axis of the floret, at the base of the floret leading to a projection (Maze et al. 1971, 1972; Mehlenbacher 1970; Kam 1974; Kam & Maze 1974) within which the cells are heavily sclerified. Cells of the lemma, especially in *A. hendersonii* and *A. wallowaense* and to some extent in *A. lemmonii* are also sclerified. Even though that feature was not measured here, it offers another demonstration of the developmental complexity of the floret.

Awn length, too, is developmentally complex; the awn is the first thing initiated in the formation of the floret and its differentiation from the lemma occurs later in development. Its growth in length is a combination of cell division, apically early in its development and sub-apically later, and cell enlargement, which appears first in apical cells. Growth in length is limited leading to the shorter awns in *A. hendersonii* and *A. wallowaense*; growth in awn length is greater in *A. occidentale*, *A. nelsonii* and *A. lemmonii*. Another contributor to the developmental complexity of the awns of the Stipeae is the sclerenchyma with eccentric lumens that surrounds the vein in the awn (Maze 1972). This tissue is implicated in the twisting and straightening of the awn of the Stipeae with hydroscopic changes (Murbach 1900) and is much better developed in *A. lemmonii*, *A. occidentale* and *A. nelsonii*. As a further indication of the developmental intricacy in the awn of the Stipeae, in those awns with well developed sclerenchyma it starts to differentiate much earlier than surrounding tissues (Maze et al. 1971).

Floret width, also, is developmentally complex since it is the result of two developmental events, the spread of the awn-lemma primordium around the floret apical meristem followed by subsequent marginal growth in the lemma. That marginal growth is made more complex through the thickness of the lemma, the result of periclinal divisions in what could be called the flank meristem of the developing lemma margins.

A strong correlation between allometric coefficients, representing ontogeny, and a phylogenetic classification, representing evolutionary history, argues for a relationship between the two phenomena. It is

tempting to resurrect the idea of a causal relationship between ontogeny and phylogeny (see Gilbert 2003 & Lovejoy 1959 for a history of such ideas). However, there is a problem with such an argument, the conceptual and empirical gap between the idea of a causal relationship between ontogeny and phylogeny and the currently popular mechanism proposed for evolution, natural selection favoring certain non-directed (often called random) variants, is large. And the idea of ontogeny driving phylogeny does not enjoy a well-established mechanism, even in most modern evo-devo studies that stress how those changes occur or the description of those changes.

But, such a disconnect is not a part of all modern evo-devo studies. Müller and Newman (2005b) and West-Eberhard (2005) argue for environmentally induced developmental events as the origin of novelty. There are a couple of interesting points from their argument. First, Darwin (1859) posited at the origin of at least some variation as from the conditions of existence, i.e., the environment, as did Lamarck (1809). Second, the ideas of West-Eberhard (2005) and Müller and Newman (2005b) would seem to be an expression of Waddington's (1953) genetic assimilation or the Baldwin effect, i.e., the incorporation of plastic traits into DNA. Recently Pigliucci and Murren (2003) argued in favor of the Baldwin effect as a source of evolutionary change. Pigliucci (2007) has also argued for an extended evolutionary synthesis that includes such phenomena as phenotypic plasticity and epigenetic inheritance, both which have a developmental basis. And Jablonka and Lamb (1995) and Steele et al. (1998) have described putative molecular mechanisms whereby environmentally induced traits can be incorporated into the DNA. Other molecular mechanisms involve methylation of DNA, as well as other chemicals such as ethyl, acetyl and phosphoryl modifications of histones (Pray 2004).

Another potentially causal relationship between ontogeny and phylogeny has been presented by Maze et al. (2005), a view derived from the argument that species are information systems (see Brooks 2001, 2002, 2010; Brooks & Wiley 1988; Maze et al. 2005). But there is a depth to the Brooks view not captured in the modern epigenetic studies or the views of Pigliuccci cited above. Those studies stressed the here and now as expressed in the material existence of individuals while Brooks arguments see the material existence of the individual as representing only part of the potential information available to an individual. That potential information, I would argue, represents the information system of the species, an information system that has captured the history of the species and carries that history forward into the future.

I find it useful to envision the information system of a species as a code, analogous to the code in a computer, that captures all the various ways in which information is expressed in the individuals of that species. Like the code in a computer, the information system of a species is known to exist when there appears a specific response in the material world to a certain action. That action, in a computer, could be striking a key; in a species that action could be the events that stimulate and allow the production of an individual.

Information expression in a species is the result of events mediated by DNA in response to environmental stimuli, both internal and external. For example, all events, molecular, cytological, histological, leading to a periclinal division in the protoderm at the apex of a grass floret would become part of the information system of that species. The same would apply to all other similar events which occur as that plant develops. The argument that environmentally mediated ontogenetic changes contribute to an expanding information system can be seen as part of Darwin's condition of existence contributing to evolution (Brooks 2010). Natural selection, which emerges from the interaction of Darwin's nature of the organism and nature of the conditions (Brooks 2010), is important as it accounts for survival, a necessary prerequisite for evolution to occur, i.e., it is necessary but not sufficient for evolution to occur.

As a result of the information expression that accrues through ontogeny of an individual, the information system of the species to which that individual belongs would expand. Much of this expansion could be traced to variation in both internal and external environments that elicit slightly different responses from the cytoplasm which will, in turn, prompt a different response from the genome. The information system of a species would also expand as the result of genetic events, viz. mutation, chromosomal rearrangements and the recombination that accompanies sexual reproduction. As the information system of the species expands

through the appearance of unique developmental events and new arrangements of DNA it becomes unstable resulting in speciation (Brooks, 2001, 2002, 2010; Brooks & Wiley 1988).

This view incorporates a common causal element into ontogeny and phylogeny. This is seen as a two phase aspect with a direct phase affecting development of an individual and an indirect phase affecting evolution. In development the direct cause of the expansion of the information system of a species is the transformation of matter, the production of information. This production of information accompanies the energy dynamics of a developing organism; the transformation of matter is the means whereby energy is processed. I note in passing that it has been shown that an increase in the amount of energy under which grape leaves develop produces an increase in the diversity of allometric coefficients which also occurs with both ontogeny and phylogeny (Maze et al. 2003a).

The relation of information expression to energy dynamics in the ontogeny of an individual, the outcome of the second law of thermodynamics in a highly organized system, offers an indirect tie between energy dynamics and evolution. The increase in complexity of the information system of a species, an increase leading to speciation, is indirectly the result of energy dynamics that are the cause of ontogeny. This is not to say that events such as mutation and recombination do not contribute to the increase in the complexity of the information system of a species; they do and perhaps may be viewed themselves as a thermodynamic phenomenon, the increase in informational entropy with the appearance of new things. These ideas are the same as those arguments first presented by Brooks & Wiley (1988). However, these views do offer a common cause for ontogeny and phylogeny and, as argued by Maze et al. (2005), such views can offer an explanation, albeit a controversial one, for incipient speciation that occurs over geographic areas greater than those occupied by single populations.

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